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RESEARCH ARTICLE

New taxa of the superorder Spirillinoida (Foraminifera) Новые таксоны надотряда Spirillinoida (Foraminifera)

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Abstract. A new recent for a miniferal genus, Raskiniella gen. nov., with the type species Spirillina plana Wiesner, 1931, belonging to the family Raskiniellidae fam. nov., order Raskiniellida ord. nov. (subclass Spirillinana: superorder Spirillinoida), is described based on samples from Antarctica. The new genus is characterised by a complex canal system that has not been previously described in any other subclasses of multichamber for aminifera with a canal system. Canals extend inside the shell wall and are partly visible as a network on the wide peripheral margin of the shell. On the dorsal surface, these canals are radially arranged, resembling ribs, and extend perpendicularly to the chamber volutions towards the centre but do not reach it. A unique feature of the described canal system is the presence of smaller canals within larger ones; sometimes internal canals can be of third or even fourth order. The majority of the canals are located within the wall of the tubular chamber, forming a network of irregularly branching tubes that frequently intertwine, varying in shapes and sizes, often with swellings. It is the collective mass of these canals that constructs the framework of the shell. The round openings with a slightly projecting outer margin, located on the ventral side of the shall, previously described as pores in S. plana, are actually the external openings of the canal system and function as additional apertures. Since the type species of Spirillina Ehrenberg, 1843, S. vivipara Ehrenberg, 1843, like apparently all other or most species of the genus, does not possess a canal system, S. plana is transferred to the new genus, which is placed in the subclass Spirillinana.

Резюме. По материалу из Антарктики описан новый современный род фораминифер Raskiniella gen. nov. с типовым видом Spirillina plana Wiesner, 1931, отнесенный к семейству Raskiniellidae fam. nov. и отряду Raskiniellida ord. nov. (подкласс Spirillinana: надотряд Spirillinoida). Его уникальная, сложная и хорошо развитая система каналов не была обнаружена ранее ни в одном из других подклассов многокамерных фораминифер, обладающих системой каналов. Эти каналы проходят внутри стенки раковины и частично видны снаружи в виде сети на ее широком периферическом крае. Они продолжаются на дорсальной поверхности раковины в виде ребер, идущих в радиальном направлении к центру перпендикулярно виткам камеры, но не доходящих до него. Уникальной особенностью обнаруженной системы каналов является наличие каналов меньшего размера внутри больших, иногда третьего и четвертого порядка. Основная масса каналов расположена в стенке трубчатой камеры как система беспорядочно ветвящихся, часто переплетающихся трубок различной формы и размера, часто со вздутиями, и именно их масса формирует каркас раковины. Округлые отверстия с несколько выступающим наружным краем, расположенные на вентральной стороне раковины и описанные ранее у S. plana как поры, на самом деле являются наружными отверстиями каналов и функционируют как дополнительные устья. Поскольку типовой вид рода Spirillina Ehrenberg, 1843, S. vivipara Ehrenberg, 1843, как, по-видимому, все остальные или большинство видов рода, системой каналов не обладает, S. plana помещен в новый род подкласса Spirillinana. **Key words:** systematics, shell ultrastructure, unique canal system, additional apertures, Foraminifera, Spirillinana, Spirillinoida, Raskiniellida, Raskiniellidae, *Raskiniella*, new taxa

Ключевые слова: систематика, ультраструктура раковины, уникальная система каналов, дополнительные устья, Foraminifera, Spirillinana, Spirillinoida, Raskiniellida, Raskiniellidae, *Raskiniella*, новые таксоны

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Introduction

This paper describes the ultrastructure of specimens previously identified as Spirillina plana Wiesner, 1931. These specimens were acquired from Antarctic sediments collected in 1996 by the German vessel "Polarstern" and previously examined from a faunal perspective (Mikhalevich, 2004, 2009; Mikhalevich & Bozhenova, 2018). In those studies, as well as in many others dealing with Antarctic materials (Wiesner, 1931; Heron-Allen & Earland, 1932; Parr, 1950; Lipps et al., 1972; Violanti, 1996; Majewski, 2005, 2010, 2013; Majewski et al., 2023a, 2023b; and many others), specimens identified as S. plana were considered as typical representatives of the genus Spirillina Ehrenberg, 1843. They have a pseudo-twochambered test with a long, enrolled, tubular second chamber that is mostly planispirally coiled. The calcareous wall has numerous pores that are flush with the surface. When viewed under a light microscope, the shell walls of the type species of Spirillina, S. vivipara Ehrenberg, 1843, appear relatively smooth on its dorsal and ventral sides as well as its Fperipheral margins. In contrast, the shell walls of S. plana instead exhibit rough textures on all surfaces, which have been considered as some kind of sculpture. The results of our research are presented and discussed below.

Material and methods

The material examined includes 28 specimens taken from samples collected off Antarctica in the Cape Norvegian area of the Weddell Sea during a 1996 expedition of the German vessel "Polarstern". The samples were obtained at Station 2 located at 71°18′60″S, 12°25′40″W, at depths of 181–253 m, on 22.II.1996, using a Multibox corer measuring 9×0.024 m² in size. The specimens examined are deposited at the Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia (ZISP).

Before microscopic examination, the foraminiferal shells were rinsed in filtered fresh water and dried using a Hitachi critical-point dryer HCP-2. Eight specimens were subsequently mounted on stubs, coated with coal coater, and initially viewed under a Hitachi S-570 scanning electron microscope (SEM), and later using a FEI Quanta 250 SEM at the "Taxon" Research Resource Centre of the Zoological Institute of the Russian Academy of Sciences in St Petersburg. The range of magnifications utilised during the studies varied from ×70 with a light microscope up to ×1500–2000 and ×8000 with an SEM.

Results

Morphology of the canal system of *Raskiniella plana*, comb. nov.

A. Details seen on the dorsal shell surface and the peripheral margin. Electron microscopic studies revealed an unusually complex shell structure of the specimens examined. The shell structure of the species previously identified as Spirillina plana is composed of complex networks of tubular features that we describe here as canals. These features were unexpected in this otherwise primitively organised shell, which consists of a proloculus followed by a long tubular chamber that is not subdivided into chambers or chamberlets. The complex network forms a mesh of straight and curved canals of varying widths, which can be seen along the entire peripheral margin of the shell (Figs 1A–E, 6A). Previously, this mesh was considered to be sculptural (Wiesner, 1931; Parr, 1950; and all subsequent publications). The network of canals extends as nearly parallel features on the surface of chamber volutions, as seen on the dorsal shell surface (Figs 1A–E, 3A, C, E, 6B–F).



Fig. 1. Surface details of the shell of *Raskiniella plana* (Wiesner, 1931), **comb. nov. A**, dorsal surface view (×70); **B**, magnified part of the image A, showing subcircular openings of the canals to the left near the centre and the elongated radial canals extending nearly to the centre on the right; **C**, peripheral view (×1500) showing locations of close-up images D, E and F, and example pore openings (p and arrows); **D**, smaller canal tubes branching from radial canals (indicated by arrows) and a pore (p); **E**, mesh of peripheral canals partially extending on the dorsal shell surface, also subcircular additional apertures (*aa*) on the upper wall of radially extending canals (indicated by arrows); **F**, elongated openings between secondary canal tubes branching from the radially extending primary canals, likely functioning as additional apertures (*aa*). Scale bar: 300 μ m (A).

The canals extend radially from the centre to the periphery (Figs 1A–E, 3A, C, E, 6A–F), enlarging towards the periphery. The canals of the peripheral volutions are the largest and generally best preserved, while those of the central volutions are mostly destroyed (Figs 2A–D, 4, 6D).

The network of canals includes primary, secondary, and tertiary tubular structures that are progressively smaller, while also displaying swellings or outgrowths. Secondary canals commonly branch out from the sides of the radially positioned canals. In addition, outgrowths of spherical, pearlike, or somewhat elongated shapes occur (Figs 3A, C, D, 6E). We refer to them as fruit-like outgrowths because they appear to hang like fruits on very thin tubular stalks (Fig. 3C), either singularly or sometimes in rows along the lower margins of the radial canals, closer to the shell surface (Figs 3C, 6E). At the free-hanging ends of such fruit-like branches, a second small sphere often can be seen (Fig. 3C, br), resembling the start of a rosary canal where the wider parts are connected without a neck (Fig. 3C, *wrc*). In some instances, newly formed rosary canals branching from a radial canal appear more elongated, with elongated swellings connected to each other by thin necks of varying lengths (Fig. 3C, erc). Small fruit-like structures are also sometimes seen inside the radial canals. One such outgrowth extending from a radial canal was larger than the others (Fig. 3A, C, D) and was found broken into two parts showing an extremely interesting interior (Fig. 3D): small, similar fruit-like outgrowths were hanging inside on the inner wall (Fig. 3C, *if*). These were also divided into two parts, similar to the larger spherical outgrowth containing them. These smaller inner spheres and the larger outer sphere were black inside, either due to the direction of light or for some other reason. The opposite half of the broken sphere was not as dark, and the pores on its inner surface were tiny (Fig. 3D). The details of the shell-wall ultrastructure will be described in a separate article. Small fruit-like spheres are often easily detached due to their very thin tubular "stalks" and can be frequently observed lying freely on the shell surface. These could be mistakenly considered foreign particles.

In many of these radial tubes, secondary canals of smaller diameter can be seen branching from both sides. These outgrowths may appear occasionally or at regular intervals (Figs 1C, D, E, 6E, F). They vary in width and often branch. Radial canals irregularly anastomose with one another; they vary significantly in width, length, and the number of smaller branches (secondary canals), although most branches are relatively short (Fig. 1C, D, E). Usually, secondary canals are thinner than the canals from which they originate and those they connect to, although sometimes they can be rather wide (Fig. 2B).

Where the shell surface is damaged, interior features of the radial canals can be seen (Fig. 2A, C, D), such as tubular structures (secondary canals) within the primary canal. Sometimes, outgrowths surround the inner secondary canal and connect it with the inner surface of the primary canal (Figs 2D, *arrow*, 4, 6D).

Endings of secondary canals that occur inside the larger radial canals can be seen at the perpendicular endings of the primary canals (Figs 3A, B, F, 6C). They are situated closer to the centre, but not around the entire centre. For example, as seen in Fig. 3A, such endings are evident, while on the opposite side of the upper shell surface to the right, elongated radial canals extend to the proloculus (Fig. 1B). In some places (Figs 3A, B, F, 6C), these endings resemble the "pores" that are slightly elevated above the shell surface at the ends of the radial tubes on the lower (ventral) shell surface (Fig. 7C). In some of them, endings of one or several inner canals can be seen, sometimes three or four, or rarely up to five (Fig. 6C). These canal endings on the upper shell surface may serve as additional apertures similar to the external openings of the canal system in higher Rotaliata (see below). At higher magnification, smaller pore openings can be observed in the transverse view of the circular wall outline of both the outer and inner canal tubes (Figs 3F, upper arrow, 6C, upper arrow), which are the endings of the thinnest canals. These structures could be named canaliculi; however, since the term is commonly used for the small canals in Textulariata, which have a significantly different shell structure, we refer to them as microcanals.

In some areas, naturally occurring breaks in the surface of the larger radial tubes reveal perpendicular subdivisions along their length (Figs 2,



shell of Raskiniella plana (Wiesner, 1931), comb. nov. A, view (×1500) of a portion with radial canals of earlier volutions extending to the periphery; the broken surfaces of some of them reveal the surface of the inner canals of the second order, occasionally even of the third order (indicated by arrow) within them; **B**, magnified view of the image A, showing a rather wide anastomosis between the two parallel canals (indicated by arrow); C, magnified view the image A, showing a third-order inner canal, with the circuits of the two previous canals above it (indicated by arrow); D, magnified part of the

shell, showing small, thin perpendicular canal connections between the inner and outer radial canals (indicated by arrow). Scale bars: 50 µm (A, D).

6C). At higher magnification, micropores oriented perpendicular to the primary (outer) and secondary (inner) canals are observed (Fig. 4B-E, G. arrows), indicating penetration of the wall in both longitudinal and transverse directions. Additionally, radial extensions are observed within the primary canal, connecting it with the inner canal in some transverse views (Fig. 6E, arrows along the radial canals). Small inner and outer canals often originate from the outer surface of the larger ones as very narrow tubular features that rather sharply widen at their ends (Fig. 6F, *left arrow*) or spherical swellings resembling some fruit hanging on their narrow ends (Fig. 3C) (see above). The initial diameter of a primary canal may determine the diameter of future canals (secondary, tertiary, etc.).

B. Canal system openings on the ventral (lower) shell surface. These features are described below (see part D), as they serve as additional apertures.

C. Details of the canal system in the inner shell wall. The broken apertural end of the shell revealed the details of the inner shell surface (Fig. 5). The entire thickness of the shell wall is formed by the tight mesh of intertwined, irregularly branching canals of different shapes and sizes, all of them comprising nearly the entire shell frame. This structure provides integrity to the shell even when fragile elements of the outer shell wall are broken. These inner shell-wall canals, together with the outer radially directed canals (with their additional apertures clearly visible in Fig. 5B, C), form the canal system that is characteristic of the species examined and principally distinguish its shell walls from the simple, smooth walls characteristic of the genus Spirillina.

Canals inside the shell wall may be of tubular or irregular tubular shape with strong swellings (Fig. 5B–D), rosary-like shape with rather wide parts joined closely without necks (Fig. 5C, D), and more elongated parts joined with each other by necks (the main mass of such ones can be seen in Fig. 5B). Small radially-oriented canals can be seen between the tightly packed elements of the outer shell wall and the remaining thickness of the wall (Fig. 5C, arrows on the right side).

Free space is abundant between the inner wall canals (Fig. 5B–D), which presumably was avail-

able for cytoplasm. Pores can also be seen in other locations (Fig. 5C). A row of transversely cut canals situated close to each other is seen in Fig. 5D, 1c, rather than one canal with perpendicular subdivisions, as it may appear at first glance. Similar wall construction was sometimes seen inside the radially directed canals of the outer shell surface. These canals may play a special role in the circulation of shell cytoplasmic processes. Unfortunately, nothing is known yet about the functioning of this species when alive. This type of canal, as well as canals positioned radially from the periphery towards the proloculus, appears to be somewhat regularly located in this species. However, the location of all other canals, their branching patterns, and additional openings (as described below) seem to be highly variable and randomly distributed.

D. Details of the apertural system. The main aperture of the species examined is represented by the open end of the tubular chamber, similar to that of *Spirillina vivipara*, but it is noteworthy that the species examined has a variety of additional apertures.

(1) One type of aperture is represented by the oval or circular open endings of canals that cover the entire ventral (lower) surface of the shell (Figs 6A-b, 7C) and by fewer multiple canal endings on its dorsal (upper) surface near the proloculus (Fig. 3A, B, F). Those on the ventral surface were previously described as "pores" (Wiesner, 1931; Parr, 1950), but no similar structures were previously found on the dorsal surface. The walls of both types of additional apertures are somewhat prominent above the shell surface. However, the additional apertures on the ventral surface have some distinctive features. They are multiple, somewhat smaller in size, and usually contain only one canal tube inside. In contrast, those of the dorsal shell surface mostly contain two or three, or even more inner canal tubes, rarely only one (Figs 3A, B, F, 6C). In the shell wall of the latter, smaller openings of the transverse cuttings of the thinnest, longitudinally oriented canals (microcanals) can also be seen (Figs 3B, F, 6C). These types of additional apertures on the dorsal side of the shell are only occasionally present, while on the ventral side, they occupy the entire surface, forming circular rows. Sometimes their openings appear elongated



Fig. 3. Surface details of the shell of *Raskiniella plana* (Wiesner, 1931), **comb. nov. A**, dorsal surface view (×1600) of the shell area near the shell centre; at the lower right, a group of slightly protruding, irregularly oval, or subcircular outer endings of canals with the openings of their inner canals contained within them (arrows); openings

as if they were cut obliquely (Fig. 6A-b). Occasionally, rather thin elongated rosary canals with elongated swellings and narrow necks between them (elongated rosary-like canals) could also be seen (Fig. 7C, lower left corner).

(2) Another type of aperture is clearly seen at the peripheral margin of the shell as openings in the peripheral canal mesh (Figs 1A, B, 6B).

(3) Some radial canals situated on the shell surface also form additional apertures at their ends, which are often visible when they are cut or broken. These may have fissured (Fig. 5B) or arcuate shapes (Figs 5C, 7B). Several openings of their small inner canals can often be seen inside such apertures (Fig. 7B).

(4) On the smooth, rather thick surface of radially-directed canals on the dorsal surface, occasional openings of subcircular, oval, or similar shapes may irregularly occur (Fig. 1C–E). Sometimes, these openings on the canal surface can be situated on a low cone (Fig. 6E, F) or seen on the canals inside the shell (inner apertures) (Fig. 6G). In one case, a flower-like additional aperture was seen at the end of the canal tube, with elongated fissures surrounding the central circular opening, resembling petals around a flower centre (Fig. 7A).

(5) Sometimes, openings between the branching canal tubes also serve as additional apertures, either inner or outer depending on their disposition (Fig. 1F).

Thus, five types of additional apertures were found in this species. Their characteristic features

of variable shape and position, irregular nature, and lack of fixed regularity in geometrical order, as seen in other foraminiferal taxa, are surprising. Not only is the number of their types striking, but also the variability of their shape and position is also remarkable. The presence of additional apertures in foraminiferal shells is an advanced feature; however, it is extremely rare to find two types of additional openings. The species studied has five additional apertural types, which indicate its progressive morphological development and evolutionary advancement. According to the description of the type species of the genus, S. vivipara Ehrenberg 1843, and literary data on other species of the genus, no canal system is found in true members of the genus Spirillina.

Taxonomy

The highly developed and specialised canal system is the primary unique feature of the studied specimens. These features provide the basis to distinguish them not only as representing a new genus distinct from other representatives of the order Spirillinida, but also as representing a new family and even a new order of the superorder Spirillinoida, subclass Spirillinana. The development of a system of such a complex level of organisation as this canal system serves as the basis for the separation in other high-ranking groups of the Foraminifera.

of their smaller inner canals and the opening with the two inner canals can be seen at the base of the right arrow; **B**, magnified part of the image A, showing the canal opening with an inner canal opening of the second order with its smaller inner canal of the third order (c upper arrow); the opening of transverse cutting of microcanal (upper arrow) in the wall of the inner canal of the second order, also small rosary canals at its outer surface are visible (two parallel arrows); C, magnified part of the image A, showing small canals next to the larger radial canals, having different forms: tubular, rosary canals (brc - beginning of rosary canal, erc - elongated rosary canal, wrc wide rosary canal), fruit-like canals (fc), inner fruit-like canal (if); inner rows of small fruit-like inner canals are visible in the larger fruit-like canal at the lower left, along with the dark inner surface of the left half of that feature; **D**, magnified view of the larger fruit-like canal visible in the lower left part of the image C, showing smaller second-order fruit-like canals hanging on the upper part of the larger fruit-like canal are also split, revealing their inner dark wall similar to the inner dark wall of the outer canal (indicated by left arrow); on the inner wall of the opposite half of this larger fruit-like canal, the openings of the smallest microcanals can be seen as pore openings (indicated by right arrow); E, magnified view of the image A and the right part of the image C, showing a small tubular canal extending from the side of the radial canal (*lctc* arrow) and additional apertures (aa) in the larger tubular canal (upper arrow point) and in the wall between the canals (upper arrow tail); F, magnified part of image A; upper arrow indicates openings of transverse cuttings of microcanals running along the wall of the canal opening on the dorsal shell surface; lower arrow shows occasional openings on the smooth wall; at the lower left, the canal ending reveals three openings to the canals inside. Scale bar: 50 µm (A).

Phylum **Foraminifera** d'Orbigny, 1826 Class **Spirillinata** Mikhalevich, 1992 Subclass **Spirillinana** Mikhalevich, 1992 Superorder **Spirillinoida** Hohenegger et Piller, 1975 Order **Raskiniellida ord. nov.**

Diagnosis. Shell calcareous, pseudo-twochambered, with proloculus and subsequent undivided tubular second chamber, coiled planispirally, with unique canal system seen on its surface as peripheral mesh of canals (Fig. 1C). Radial canals extending from periphery on dorsal surface towards proloculus but not reaching it (Figs 1A-E, 2A-C); somewhat elevated opened endings of canals occupying entire dorsal surface of shell (Figs 6A-b, 7C) and extending inside wall as irregularly ramifying and interweaving tubular canals possessing swellings of different sizes, shapes and degrees, with varying diametres (Fig. 5B-D). Unique structures occur inside larger canals, including inner smaller canals of second, third and rarely even fourth order (Figs 2A-D, 4B-G, 6C, D). Main aperture terminal, at open end of chamber on peripheral margin. Several types of additional apertures also present: as multiple subcircular openings covering entire ventral surface of shell (Figs 6Ab, 7C), as openings in peripheral mesh (Fig. 6B), as space between tubular canals (Fig. 1F), or as occasional openings in upper wall of radial canals (Fig. 1D).

Comparison. The order Raskiniellida ord. nov. differs from the order Spirillinida Hohenegger et Piller, 1975 (the only previously established order of the superorder Spirillinoida characterised by planispiral coiling) by possessing a unique, intricate, branching canal system that runs through the shell wall, forming its frame and partially opening on the shell surface. In contrast, the shell surface of the species of the order Spirillinida is completely smooth. The new order differs from the order Spirotrocholinida Mikhalevich, 1993 (the only order assigned to the superorder Spirillinoida in which canals have been found; Fig. 7C) in its planispiral arrangement of the second chamber, as opposed to a trochoid arrangement. Additionally, the new order is distinguished by a more complex canal system of a different type that extends into the shell wall. In

comparison, the order Spirotrocholinina is characterised by a simple tubular canal extending into the deep umbilical cavity between chambers but not inside them (Fig. 7C). All the other orders of this superorder are of trochoid form and can thus be easily distinguished from the new order, which is characterised by a planispirally coiled shell. Additional features that distinguish the new order from other orders of Spirillinoida are provided in a key below.

Key to the orders of the superorder Spirillinoida

The authors recognise five orders within the superorder Spirillinoida: Cymbaloporida Mikhalevich, 2013, Patellinida Mikhalevich, 1992, Raskiniellida **ord. nov.**, Spirillinida Hohenegger et Piller, 1975, and Spirotrocholinida Mikhalevich, 1993.

- 1(4). Shell flat, planispirally arranged, pseudo-twochambered; second chamber tubular, not subdivided; lower (ventral) shell side without umbilicus.

- 4(1). Shell conical, trochospirally arranged.
- 6(5). Shell multichambered.
- 7(8). Shell trochoid, with early part sometimes having a whorl or several whorls of trochospirally coiled tubular chamber, later whorls mostly with a few chambers (three or even two), often subdivided by radial septula; umbilical side flat or slightly convex, closed; aperture at centre of umbilical side, looking like narrow slit of variable shape depending on form of apertural plate being variable in outline (S-shaped, slit-like or of other shape)... **Patellinida**
- 8(7). Shell trochoid, with a few or multiple chambers; later chambers sometimes in cyclic series in flat or conical layer; umbilical area sometimes slightly



Fig. 4. Surface details of the shell of *Raskiniella plana* (Wiesner, 1931), **comb. nov. A**, dorsal surface near the centre, showing the locations of images B–G, providing details of the destroyed ra-

dial canals on the dorsal surface of the shell (×2500); **B**, **C**, **D**, **G**, radially extending elements (microcanals) in the canal walls (indicated by arrows), here and there are small dark openings of the same diameter, which are transverse cuttings of similar microcanals; **D**, small circular openings along the left side of the cutting (transversely cut microcanals, left arrow) and radial elements (longitudinally extending microcanals, right arrow); **E**, small circular openings of transversely cut microcanals along the left side of the cutting (indicated by small arrows), and just below them are longitudinally extending cuttings of microcanals; large arrow indicates three layers of the wall seen at destroyed radially extending canals (one outer and two inner ones of the second and third order); **F**, several layers of the wall of the outer radially extending canals (indicated by arrow); **G**, three layers of the wall of the outer radially extending canal with inner canals of the second and third order clearly visible at the upper and right sides of this photo; the radially extending small microcanals connecting the outer and inner layers are also clearly seen (arrow). Scale bar: 40 µm (A).

Family Raskiniellidae fam. nov.

Diagnosis. Shell pseudo-two-chambered, with proloculus followed by an undivided tubular sec-

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ond chamber, coiled planispirally. Unique canal system present, extending from inside to outside shall wall and represented by mostly irregularly branching tubular primary canals possessing swellings of different sizes formed along their length. These canals often with inner canals inside them, those being of tubular or subspherical shape (Figs 1–5). These inner canals sometimes of second or even third order (Figs 3, 4, 6C, D). Aperture terminal, at open end of tubular chamber; several types of additional apertures present.



Fig. 5. Surface details of the shell of *Raskiniella plana* (Wiesner, 1931), **comb. nov. A**, locations of the images B-D, and a view of the broken apertural part of the shell with the openings of the radially extending canals on the dorsal side visible on the right side of this image, and less developed smaller canals on the ventral side of the shell (×2000); **B**, fissure-like vertical openings leading to radially extending canals on the upper side of the shell (indicated by arrows on the right), black opening at the upper side is an additional aperture (*aa*), small black openings are free spaces between the elongated rosary canals (*r*) of the inner shell wall, forming a single net (indicated by arrow at the lower centre); **C**, arcuate canal openings of the broken margin of the ventral shell side with tightly packed, radially

Composition. At the time of publication, only one family is known in the order, and only one genus is known in the family.

Genus Raskiniella gen. nov.

Type species: Spirillina plana Wiesner, 1931.

Diagnosis. Shell flat (Figs 1A, 6A), pseudotwo-chambered, with globular proloculus and subsequent undivided tubular second chamber, coiled planispirally; with complex disordered canal system consisting of network of irregularly branching tubular canals of unique structure inside shell wall (Fig. 5B-D), not visible externally. Mesh of peripheral radial canals located on and into wall of dorsal (upper) shell surface (Fig. 1A–E). Some of canals extending inside shell wall visible externally on shell surface as a mesh on wide peripheral margin (Fig. 1A–C), from where they extending radially toward centre as linear structures on dorsal shell surface (but not reaching proloculus) (Fig. 1A, B). Other parts of canal system only visible at transverse breaks in chamber wall and on inner surface of wall (Fig. 5). Canal tubes of different length and diameter, with significant swellings, sometimes resembling a series of rosary beads (Fig. 5D), or of irregular shape, sometimes bent at various angles, often with additional canal structures outside and inside them, having tubular, pear-shaped, or subspherical shapes (Figs 2, 3, 5, 6C, F). Inner canals sometimes of second or even third (rarely fourth) order, one inside other (Figs 2, 3, 4, 6C, D). Canals opening on lower (ventral) side of shell as subcircular or oval short terminations slightly elevated above shall surface; sometimes canal endings present on dorsal surface near centre (Fig. 3C). In outer canals with secondary (and tertiary) canals, smaller ends of these inner canals also visible inside encircling endings of larger primary canal tube (Figs 3B, F, 6C). Aperture terminal, at open end of tubular chamber; additional apertures of several types: (1) in cells of peripheral mesh network (Figs 1A, C, 6B); (2) as singular openings elevated on a small cone (Fig. 6G) or, more rarely, groups of circular openings on slightly convex cone at angles where radial canals connected with mesh network (Fig. 6E, F); (3) occasionally, subcircular openings on radial surface of a canal (Fig. 1D, E) and sometimes at canal ends as flower-like structure (Fig. 7A); (4) as openings between branches of canals (Fig. 1F); and (5) fissure-like or arcuate openings at ends of radial canals (Fig. 5B, C).

Notes. The new genus differs from all other spirillinids in the presence of a complex canal system with a pattern and position that were not previously known. Peripheral and radial canals of *Raskiniella plana*, **comb. nov.** were originally described as "shell sculpture", and the canal openings on the ventral side were interpreted as pores. Sometimes, inside a larger and wider canal, inner canals of not only the second order but also the third order are formed. Scanning electron microscopy of specimens is essential for revealing their complex inner structure.

Other spirillinids with similar outer shell "sculpture" likely also belong to this new genus. Examples include the Antarctic taxa S. obconica var. dorsoserrata Parr, 1950, S. radiosa Parr, 1950, and S. dimidiata Wiesner, 1931, species described from the Caribbean Sea as S. heterostriata Mc-Culloch, 1981, S. fimbriata McCulloch, 1981, S. discors McCulloch, 1981, and S. complanatiformis McCulloch, 1981, and possibly some other species that were previously assigned to Spirillina. Our data support the supposition of Rigaud et al. (2023) regarding the possible internal structure of the radial ribs in another superorder, the aragonitic involutinid genus Hensonina Moullade et Peybernès, 1974 (superorder Involutinoida). The group of Spirillina species with an "outer shell sculpture" and "protruding pore openings" on the ventral shell side very likely belongs to our new genus. The type species of Spirillina, S. vivipara, differs in that it lacks a canal system. Other species that lack "sculpture", such as S. obconica Brady, 1879 and S. perforata (Schultz, 1854), likely also lack a canal system.

directed microcanals at their margins (indicated by arrows on the right side); left arrow shows widened canal tube; **D**, shell wall of the broken ventral side of the shell as viewed from the broken aperture; in the upper part of the image, two parallel lines of canals lined up in two rows (*ic*, *lc*) and somewhat deeper anastomoses (*a*) between these two rows (two parallel arrows in the right); in the lower part of the image, there is a transversely trending broken canal (*bc*) and an arcuate first-order canal with open ends (indicated by arrow at the lower left). Scale bar: 50 μ m (A).



Fig. 6. Shell of *Raskiniella plana* (Wiesner, 1931), **comb. nov. A**, views of the shell: the dorsal side at \times 75 (a), the ventral side at \times 70 (b), and the peripheral view at \times 70 (c); **B**, additional apertures in the mesh of the peripheral body (indicated by arrows); **C**, several canal endings, subcircular in outline on the dorsal shell surface in the area close to the centre, show different numbers and sizes of the inner canals; multiple microcanal openings are indicated by arrows; **D**, radial canal on the dorsal shell surface with a broken upper wall with two elongated canals visible inside and very thin canals connecting the inner canals with the outer one (indicated by arrows); **E**, radial canals on the dorsal shell surface, with smaller canal branches of cylindrical (indicated by arrow on upper left) and subspherical (arrow on lower right) shapes and a group of additional apertures (arrow on upper right) at the border of the dorsal shell surface and the peripheral margin ; **F**, magnified view of image E, showing a group of additional apertures (indicated by upper arrow in E) at the border of the dorsal shell surface and the peripheral

Etymology. The genus name is given to honor the well-known historian and archivist David Raskin, who devoted a significant part of his publications to the history of science, some of them in co-authorship with V.I. Mikhalevich.

Composition. Currently the genus includes only one species, *Raskiniella plana* (Wiesner, 1931), **comb. nov.**

Raskiniella plana (Wiesner, 1931), comb. nov. (Figs 1–6, 7A–C)

Spirillina tuberculata var. plana Wiesner, 1931: 128, pl. xxi, fig. 252.

Spirillina plana: Parr, 1950: 349, pl. xiii, fig. 9.

Material examined. 28 specimens, **Weddell Sea**, Cape Norvegian, Station 2, 71°18′60″S, 12°25′40″W, depths of 181–253 m, 22.II.1996 (ZISP).

Distribution. Antarctic and subantarctic areas. Recent.

Discussion

During the evolutionary history of the phylum Foraminifera, various integrative systems have emerged to enable communication among the cellular components enclosed within the hard shell and with the environment. These systems developed from the simplest form, such as the successive chain of communication via inner apertures among multi-chambered forms, then somewhat more advanced tunnels and stolons, and integrative apertural systems, up to the most advanced of them, that is, canal systems achieving their utmost complexity. These systems are well studied in numerous higher representatives of the class Rotaliata Mikhalevich, 1980. In the class Spirillinata Mikhalevich, 1992*, taxa with canals are less well-known and were discovered much later. The role of canals is especially important as a system

that supplies the cell with oxygen and allows it to be transported throughout the entire shell cytoplasm (Hottinger, 1978), resembling the role of blood vessels in mammals (Mikhalevich, 2000, 2013a, 2013b, 2021).

In both classes (Rotaliata and Spirillinata), integrative systems emerged in complex multichambered shells as a way of overcoming the compartmentalisation of the test (Mikhalevich, 2000, 2008, 2013a, 2013b, 2021). In the class Spirillinata, canal systems have been much less studied. They were previously only known in multi-chambered or tubular-trochoid shells. Canals have occasionally been described among fossil trochospiral forms (Hottinger, 1976, 1978; Mantzurova & Gorbatchick, 1982; Piller, 1983; Azbel, 1986). A scientific team (Rigaud, 2012; Rigaud et al., 2013a, 2013b, 2018, 2023; Rosales & Schlagintweit, 2015; Schlagintweit et al., 2015) published a series of significant articles on the morphology of fossil representatives of the class Spirillinata, primarily from the order Involutinida. They found new and interesting cases of the presence of canals, but mostly in multi-chambered trochospiral representatives. Nevertheless, this team successfully documented the presence of the canal system in the planispirally coiled tubular nonseptate representatives of the aragonitic superorder Involutinoida, order Involutinida (Rigaud et al., 2013a, 2015, 2023). However, due to the preservation state of the material, conducting a comprehensive study of the entire canal system on slides was not feasible. Studying such minute and complex forms in ancient sediments is challenging, requiring exceptional craftsmanship to observe such canal systems. This can only be achieved by working with thin sections. We were fortunate to find a modern specimen of the species formerly known as Spirilina plana with a significantly damaged outer shell wall, especially between canals. This damage allowed us to observe the canal system in three-dimensional detail. Such a study of the planispirally coiled, tubular, non-septate representative of the other order within the subclass Spirillinana, superorder Spirillinoida, could be conducted for the first

^{*} The authors of the present article use the foraminiferal classification elaborated by Mikhalevich (1992, 2013a) and later supported by genetic-molecular data (Pawlowski, 2000; Pawlowski et al., 2013).

margin (right arrow), and a secondary canal (indicated by left arrow); **G**, a single additional aperture elevated at a small cone (indicated by arrow) on the inner shell surface. Scale bar: 20 μ m (E).



Fig. 7. Surface details of the shell of *Raskiniella plana* (Wiesner, 1931), **comb. nov.** (A–C) and *Spirotrocholina incerta* (Svetovostokova in Myatlyuk, 1953) (D). **A**, a single additional aperture of the flower form at the end of the cylindrical canal, with the subcircular opening at the centre and several elongated slits around it; **B**, additional aperture at the end of a radial canal on the ventral shell surface showing several smaller canals inside (arrow); **C**, part of the ventral side of the shell, which is entirely occupied by the slightly protruding open canal endings of subcircular or oval outline and occasional short, narrow canals; **D**, side view of the shell (×70); **E**, diagram of a transverse section of the trochoid shell (×360) with a wide umbilical cavity, parallel transverse lamellae, and pillar in the centre; canals go under lamellae and spiral within the pillar (dotted lines). After Azbel (1986) (D, E).

time. The picture of the entire canal system, with all its details, is described.

The discovery of a unique canal system of high complexity among the more primitive pseudotwo-chambered tests with a long, planispirally coiled, tubular second chamber, among the recent calcareous representatives of the superorder Spirillinoida was totally unexpected. The canal system represents a dense network of canals that form the thickness of the shell wall and serve as a supporting element of the frame of the chamber volume (Fig. 5). Comparing the better-known canal system of the Rotaliata representatives, where the canal scheme appears in strict geometrical order, the canal scheme of the new genus appears to be more plastic, highly variable, irregularly branching, and interweaving in different patterns. The canal system of the species studied obviously evolved to overcome the boundaries between the volutions of the long tube, allowing the entire shell cytoplasm to function as a single organism. Future studies of the functioning of this unusually complex canal system by observing live specimens in culture would be of significant biological and physiological importance.

The shape and branching patterns of the canals in the examined species indicate its highly variable nature, as do other features of shell construction, such as additional apertures (see the Section D, Figs 3A, B, F, 6Ab, 7C) and the canal endings, which vary in shape and quantity on both sides of the shell (Figs 3A, B, F, 7A). The presence of five types of additional apertures (see the Section D) also indicates advanced evolutionary development of the new genus. In contrast, in the advanced genera of other foraminiferal classes, it is extremely rare for a species to have two types of apertures. Only two types of additional apertures in *Raskiniella plana*, **comb. nov.** have definite positions: those in the peripheral network and the openings of the canals on the ventral side of the shell (Figs 1A, C, 6A, 7C). The others apparently form where and when they are needed.

Raskiniella gen nov. exhibits a combination of primitive features (a simple tubular shell not subdivided into any compartments, with a terminal aperture) and advanced features. These advanced features include the presence of a complex canal system with a unique structure that facilitates communication throughout all parts of the cell, along with the presence of additional apertures. The free and variable nature of the shape, dimensions, and branching patterns of this canal system is unusually high, potentially providing the organism with a significant degree of variability and adaptability.

Conclusions

All these new structural peculiarities studied enable us to erect the new genus within Raskiniellidae **fam. nov.** and Raskiniellida **ord. nov.**, belonging to the subclass Spirillinana and the class Spirillinata. The presence of a unique complex canal system, which fundamentally differs from the canal systems in the class Rotaliata and from the only known case of the canal system in the class Nodosariata (Revets, 1989), indicates that this feature holds high-ranking significance in the diagnosis of the subclass Spirillinana and class Spirillinata.

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